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AN ANALYSIS OF THE PROPULSIVE MECHANISMS OF FISHES,
WITH REFERENCE TO SOME FOSSIL ACTINOPTERYGIANS

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Although the components of the propulsive system of fishes have been studied in great detail for years (see Nursall, 1956; Brown *et al*, 1957, for recent reviews of the literature from different aspects), there is still much debate about the mechanics of fish swimming (Szarski, 1964; Gutmann, 1966; Willemse, 1966). Nursall's commendable work on the subject fails to achieve a workable model of a swimming fish and a proper understanding of the form and function of the myomeres.

Willemse (1959) unjustly criticizes the concept of the muscle-tendon system of fishes on the basis of several false assumptions. The first of these is that the muscle-tendon system was advanced by Nursall to account for fish locomotion in general (Willemse, 1959: 589), whereas the system is said to be significant chiefly among the Acanthopterygii (Nursall: 136). Second, Willemse and Nursall assume that non-longitudinal components of forces (M_1 , M_2 , M_3 , M_4 , of Willemse, 1959) are in some way significant during myomere contraction in the motion of the fish. Since each lateral myomere is symmetrical within itself, non-longitudinal components of forces generated along one limb of a myomere are cancelled out by opposing forces generated along the opposing limb of the same myomere. Third, Willemse (1959), and apparently all other authors on the subject, assume that an axial skeleton or exoskeleton is necessary or functional in producing body flexures. Although the axial skeleton or the exoskeleton serve to modify the swimming of fish, they play no part in swimming per se. Fourth, Willemse assumes implicitly that the pattern of myomere folding is unimportant (1959: 593) whereas it has been repeatedly demonstrated (Nursall, 1956; Szarski, 1964) that the folding of the myomeres plays a very important role. Recently, however, Willemse (1966) corrected himself on this point in a very interesting contribution to our understanding of myomeres. Willemse (1959) nevertheless contributed two points worthy

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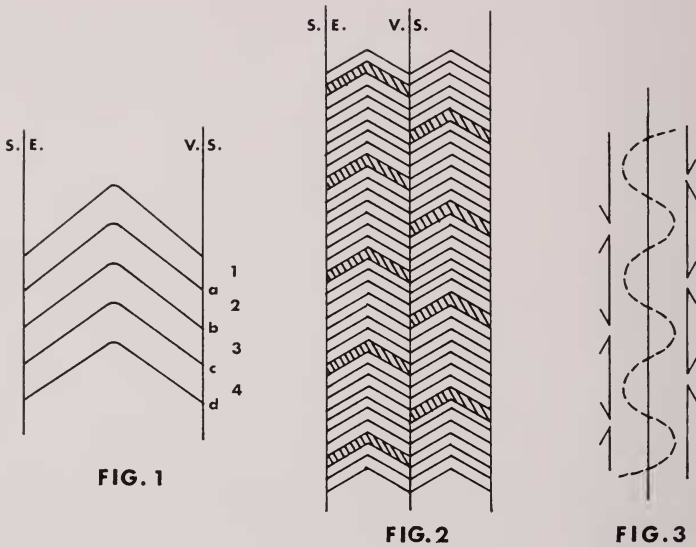


Fig. 1. Diagrammatic dorsal view of muscles of one side. Numbers refer to myomeres, letters to myoseptae. Fig. 2. Diagrammatic frontal section of epaxial musculature. Shaded segments are at maximum contraction. Fig. 3. Dorsal view of force couples and resulting flexure.

of note, namely that the septal attachments to the vertebral column are weak, and that the fish does not operate as a system of levers but in a fashion analogous to a series of alternating bimetal strips.

A bimetal strip is composed of two metals with different rates of thermal expansion, rigidly fixed to each other along a long surface. The body musculature of a fish can be looked at as being composed of two longitudinal masses, fixed to each other by the median vertical septum running the length of the fish. Each muscle mass is subdivided by myoseptae into complexly folded myomeres (Greene and Greene, 1913, and Breder, 1926, illustrate well the pattern of myomere folding). Each myomere is separately and completely innervated by one segmental spinal nerve, and by this means the myomeres retain the simplest possible pattern of innervation irrespective of myomere complexity (Szarski, 1964). Contractions of the myomeres pass as waves down the body of the fish from head to tail in forward swimming, these contractions alternating spatially on either side of the body as in figure 2. The action of a muscular segment on one side of the body (fig. 1) reveals the following chain of events: the first excitation or stimulus affecting

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the series causes myomere 1 to contract, pulling myoseptum a. anteriorly and holding it fairly rigid. The contraction stimulus passes rearward to myomere 2, stimulating this myomere to contract. Myoseptum a. (fig. 1), since it is held firmly by the contracted fibers of myomere 1, serves as the origin for the fibers of myomere 2. The contraction of myomere 2 therefore pulls myoseptum b. forward. Myoseptum c. and myomere 3 are in turn pulled forward as the contraction stimulus passes posteriorly through the fish.

As the rearward wave of contraction passes, myomeres relax and lengthen in the same sequence in which they contract.

It is to be noted that the resultant of forces produced during the contraction of a single myomere is directed longitudinally. The lateral components of forces produced on opposing limbs of each myomere all but cancel each other out. Thus the effect of contraction of a series of myomeres is to produce a longitudinal pull upon the uncontracted myomeres just back of them. Folded myomeres have the effect of producing a smooth, uniform pull throughout the width of the lateral muscle mass. This provides an extra volume of muscle fibers activated by the same nervous impulse without adding much to the cross-sectional area of the fish.

Figure 2, representing a long segment of the body of a fish, shows that a zone of maximum contraction on one side of the median vertical septum matches a zone of maximum relaxation on the other side. It is clear that muscular activity in the fish creates a longitudinal series of alternating force couples (fig. 3), as in a bimetal strip, (Will-emse, 1959) which in turn produces a sine curve. The degree of curvature produced will depend upon the number of segments involved in a single contractile wave.

Note that this system of subdivided lateral muscle masses held together by the median vertical septum, and completely lacking osseous or cartilaginous elements, is not merely a theoretical model. The leptocephalus larva of various members of the group Elopomorpha (Greenwood, et al., 1966), with a body consisting only of these components, is able (in the case of some species) to swim against powerful ocean currents, and to travel thousands of miles, using precisely this propulsive system. Leptocephalus larvae, regardless of their length, can swim with the same efficiency by using the vortices generated by swimming motions at the front end of the body (see Walters and Liu, 1967). In fact, Slaymaker (1966:7) cites leptocephalus larvae of almost negligible thickness, over four feet in length.

Both the muscle-tendon system of fish propulsion and the bimetal theory of Willemse (1959) stress the flexible vertebral column as a part of swimming. It has been demonstrated above that the axial skeleton is unnecessary for fish propulsion, and that fish can and do swim excellently with no axial skeleton at all. What then is the function of the axial skeleton? The vertebral column, rather than a structure which allows or aids flexures of the fish body, is a series of structures which tend to limit the degree of flexion possible. The ligament connections between vertebral centra will under no conditions allow the degree of flexion between segments found in the leptocephalus. Since the evolution of vertebral centra seems to have a strong selective advantage among fish, one must conclude that limitation of body flexion through the development of vertebrae was advantageous, particularly in propulsion.

The most extreme cases of vertebral restriction of lateral motion of the body of a fish occur in the caudal vertebrae of the Sailfish (*Istiophorus*) and the Marlin (*Makaira*). Elongate neural and haemal processes prevent lateral motion of the individual vertebrae in excess of ten degrees of arc (Gregory and Conrad, 1937: 11). The ultimate vertebra, the hypural fan, is a triangular plate capable of lateral motion through 180 degrees. This plate supports the entire caudal fin, and is the focus of virtually all the forces produced by the deeply folded myomeres. In these advanced percoid fishes, the initial power for acceleration from zero velocity is provided by the motion of the relatively rigid caudal portion of the body as a whole, while great speed through the water is maintained by the sculling action of the hypural fan, driving the caudal fin. The deep folding of the musculature, and the tendons that connect it to the hypural fan, give it the effect of unsegmented longitudinal muscle masses. The subdivision of the muscle and the structure of the myoseptae eliminate distortion of the fish's shape as a result of muscle contraction (Willemse, 1966).

The propulsive system of the xiphoids illustrates the acme of fish propulsive evolution. A perfectly symmetrical caudal structure provides forward thrust with no lift components. The axial skeleton channels the total effort of the muscular system into the caudal region, where it can either act for great power or for speed, with no basic change in the innervation or the pattern of the musculature itself.

The evolution of the vertebral column in fishes is the evolution of a structural complex that modifies the propulsion, enabling the fish to swim with more speed and power. All bony fish that evolved a bony

axial skeleton show modifications of this structure toward the same end: progressive specialization of the caudal region, which assumes more and more of the swimming function. The result is the formation of a functionally homocercal tail.

The earliest actinopterygian fishes, the chondrosteans, lacked a bony axial skeleton, but possessed a complete covering of articulated, rigid, bony scales covering the entire body. The body axis sloped gently upward and tapered to a point at the back end of the body. The ventral edge of the upturned body axis bore a rayed (the caudal) fin. This type of caudal structure, known as the heterocercal tail, was merely a physical and functional continuation of the body. The propulsive mechanism of the chondrosteans was basically the same as that in the leptocephalus larva, as modified by the ganoid exoskeleton and the heterocercal tail. According to Harris, 1937, and Alexander, 1965, the upturned body axis and ventral position of the caudal fin would produce a lifting force at the front end of the body in the swimming fish. The pectoral fins would partly compensate for this. The combined effect of the weight of the ganoid exoskeleton at the front end of the body and the position of the air bladder would probably have compensated in great part for the lift generated by the tail. The scales would have provided a certain amount of resistance to body flexure, sufficient to reduce the amplitude of curvature of the body, and would have correspondingly increased the power delivered to the surrounding water by the undulations of the fish.

Anguilliform motion in the chondrostean fishes would have been possible by reducing the relative size of the scales, thus reducing their effect upon lateral body undulation. This is seen among the *Tarrasziidae* (Dyne and Moy-Thomas, 1938).

The hemi-heterocercal tail of the holostean-level fishes is a slight modification of the heterocercal swimming mechanism. The caudal fin has become more definitely terminal in position. In contrast to the heterocercal condition, it displays a one-hypural, one-fin-ray relationship. The caudal extension of the body axis, which functioned as the dorsal leading edge of the caudal fin, has withdrawn to the base of the tail. The interlocking dorsal ridge scales remain as fin-fulcra to serve as the rigid dorsal leading edge of the caudal fin. Bainbridge (1963) has shown the importance of the leading edges of the caudal fin in their relationship to the motion of the remainder of the fin, among some isospondylous teleosts. The function of the hemi-heterocercal tail is to amplify lateral undulations produced by serial myomeric action.

The pycnodont fishes display only slight modifications of the basic hemi-heterocercal condition. For my example I have taken *Mesodon macropterus*, from the Kimmeridgian of Bavaria (CM¹ 4456; fig. 4). Enlarged fulcral scales based in front of the upturned body axis strengthen the dorsal edge of the caudal fin. Four hypurals support the four branching rays that form the bulk of the dorsal lobe. The bulk of the ventral lobe is made up of four rays originating from two to three hypurals, in front of which are enlarged fulcral rays originating from two hypurals. The six weak, undivided central rays are supported by hypurals so stout that they must have served as the origin for muscles connected with the dorsal lobe of the fin as well as the rays of the central lobe. The dorsal lobe of the fin and the central region operated as a unit, while the ventral lobe operated as a separate unit in sequence with the other lobe. The concentration of finrays into discrete lobes is a slight elaboration of the hemi-heterocercal condition, a pattern that varies little among the pycnodonts. The effectiveness of the compressed body form, coupled with this improvement in caudal structure evidently gave these fish enough of an advantage to compete successfully with the teleosts until the late Eocene.

Among the amioids, the eugnathid fishes, such as *Eugnathus* and *Heterolepidotus*, display the basic hemi-heterocercal condition. The Amiidae, including *Megalurus*, show the same caudal structure, unadorned by ganoid scales and rigid fin fulcra. The basically undulatory nature of the caudal fin motion can be amply confirmed by watching an *Amia calva* swim. This type of motion is ample for slow swimming, where high power or great speed are not necessary. *Amia* today is a highly successful quiet water carnivore, capable of more than holding its own against predatory teleosts (Lagler and Hubbs, 1940).

In other lines of amioids there has been considerable diversification. There is a loss of the one-to-one ratio of hypurals to fin rays, apparently because of a multiplication of fin rays, principally at the dorsal and ventral edges. A few hypural plates expand, and the fin rays of the dorsal lobe of the caudal fin span several hypurals to attach to one expanded hypural. This type of caudal-fin structure is common to all amioids related to the genus *Caturus*, a group of considerable scope and diversity. I propose to call this group the superfamily Caturioidei, after its most typical genus, and herewith define it.

All members of the Caturioidei show the principal rays of the dorsal lobe of the caudal fin originating from one hypural plate. In all but

¹ Museum name abbreviations in this article are: AMNH, American Museum of Natural History; CM, Carnegie Museum; MCZ, Museum of Comparative Zoology.

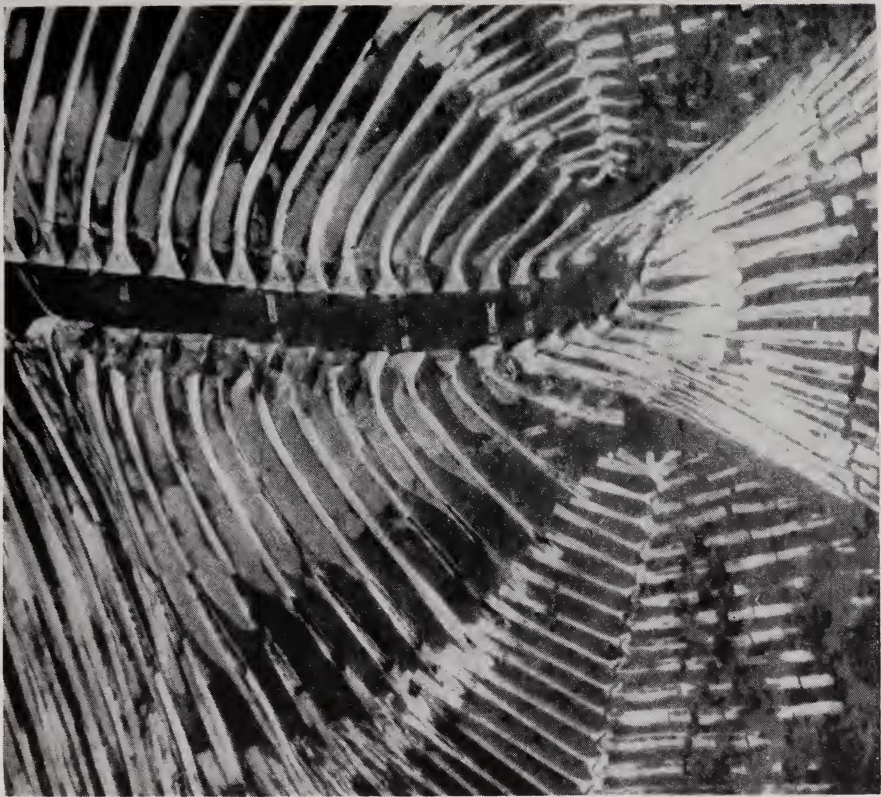


Fig. 4. *Mesodon macropterus*. CM 4456; Kimmeridgian, Solenhofen, Bavaria.

the most specialized members of the group, the fin rays of the dorsal lobe of the caudal fin pass lateral to the hypurals farthest to the rear, anchoring at or near the ventral edge of the principal hypural. Further, there are one or more devices that lock the last few vertebrae together, restricting independent lateral motion of individual vertebral segments. This may take the form of neural or haemal spines that fit together in a tongue-and-groove fashion (figs. 5 and 8), or peg-and-socket joints between haemal arches (fig. 6 and Saint-Seine, 1949: 154), or any combination of the above, within the span of the caudal vertebral series. There are many more caudal fin rays than supporting elements.

The caudal structure of the Caturioidei is best shown by that of a specimen referred to *Caturus furcatus* (CM 872; fig. 5). Neural and haemal arches and spines in the caudal region are sharply inclined backwards, to the extent that in the segments toward the rear both neural and haemal spines intertongue. Four to six expanded hypural plates form the base for the principal rays of the ventral lobe of the caudal fin. All principal rays of the dorsal lobe are supported by a single hypural plate situated along the longitudinal axis of the fish. This hypural is usually expanded into the form of a right triangle, with lateral ridges along the ventral edge. In cross section the lateral ridges give the bone the appearance of an inverted T. There may be as many as five smaller hypurals dorsal to and rearward of this main plate. The fin rays of the dorsal lobe are deeply divided along their midlines for about one-quarter of their length. In longitudinal section each fin ray is Y-shaped. The limbs of the Y lie lateral to the farthest rear, small set of hypurals and attach to the ventrolateral ridges of the largest hypural plate. The small hypurals support the few highly divided fin-rays forming the central region of the caudal fin.

The effect of the tongue-in-groove structure of neural and haemal spines, as with the interlocking processes on the caudal vertebrae of *Makaira*, is to restrict lateral motion of the individual vertebral segments, and concentrate the effect of myomeric action upon the last, unrestricted hypural plate. This skeletal adaptation supports a muscle-tendon system to move the principal hypural (Nursall, 1956: 136). The dorsal and central lobes of the tail move as a unit in the caturoid tail, because of the interlocking of the farthest rear hypurals with the rays of the dorsal lobe of the caudal fin. The ventral lobe of the tail acts as a separate unit, but is somewhat undulatory as a result of the relative independence of the few hypurals.

Pachycormus esocinus from the Upper Lias of Holzmaden shows the

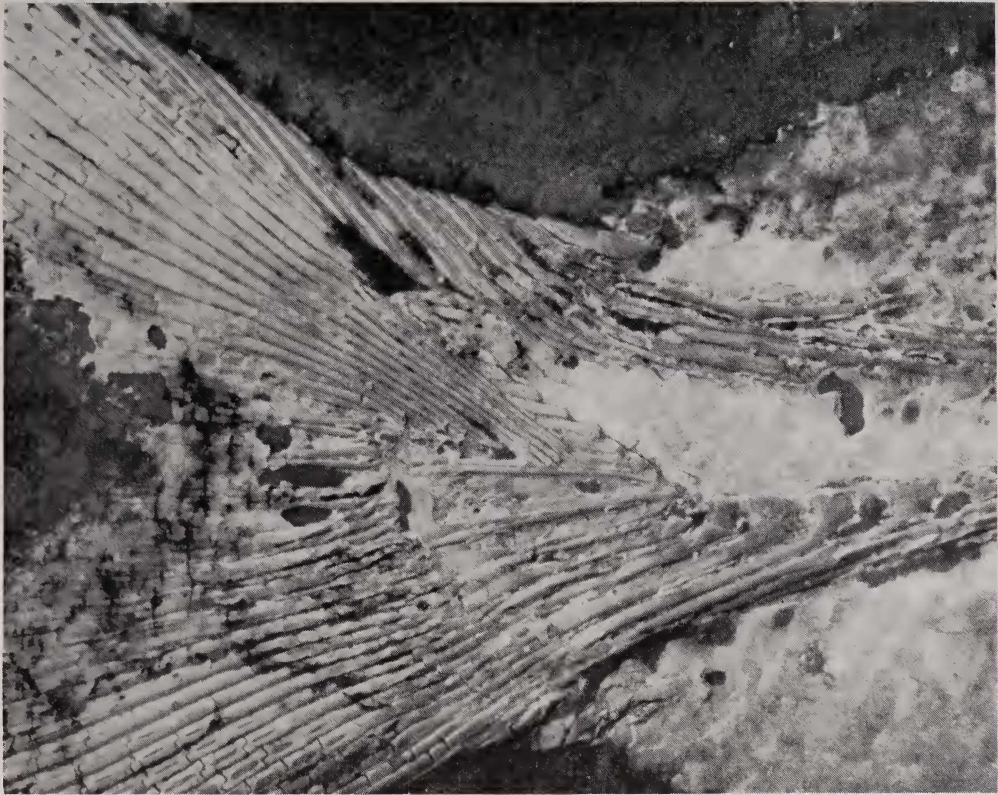


Fig. 5. *Caturus* cf. *furcatus*. CM 4701; Kimmeridgian, Solenhofen, Bavaria.

extreme of caudal skeletal modification found among the amioids. In it all principal rays of the dorsal lobe of the caudal fin originate from one fan-shaped hypural plate, attaching to its upper half. All principal rays of the ventral lobe of the caudal fin originate from the ventral half of the same fan-shaped plate and from one hypural immediately in front of and appressed to, the terminal hypural (CM 5243; fig. 8). No ossified elements of the axial skeleton are discernible dorsal to the terminal hypural on the ventral surface of the upturned body axis. There are about sixteen shorter, enlarged fulcral rays, in front of the principal rays in both dorsal and ventral lobes. During the life of the fish these attach to neural and haemal spines that fit together in a tight tongue-and-groove arrangement designed to significantly limit independent undulation. Myomeric activity was therefore confined to producing either fore-and-aft motion, via a system of tendons upon the hypural plate, or a sweeping motion of the entire caudal portion of the body. The entire propulsive system of *Pachycormus* is constructed much like that of *Makaira* and *Istiophorus*. *Pachycormus* evolved a propulsive system which differs only in detail from that of the most efficient of modern swimming teleosts, the scombroids.

A seemingly universal feature of the tails of fishes with caudal vertebral centra is the presence of at least one centrum supporting two hypural elements. This feature serves as the origin of specialized muscles controlling the action of the dorsal lobe of the caudal fin. Both *Lepistosteus* and *Amia* display this feature (Goodrich, 1933, fig. 117). The double hypural often occurs at the level at which the vertebral axis turns upward (along the posterior prolongation of the longitudinal axis of the fish). Although in *Amia* the double hypural occurs farther up along the upturned axis than usual, this seems to be the exception rather than the rule among amioids. In all Kimmeridgian amioids with vertebral centra in the upturned lobe, such as *Oeonoscopus* and *Megalurus*, at least one centrum at the base of the upturned lobe, and frequently as many as three centra, bear double hypurals.

In none of the amioids with this feature are the hypurals expanded to any greater extent than the neighboring hypurals. In fact, in none of these fish are there any adaptations for rapid or exceptionally powerful swimming. By every anatomical indicator, these fish are relatively slow swimmers of rather limited power. All of them progressed in a basically undulatory manner. It is plausible that the musculature associated with the double hypural added a degree of sophistication, necessary for undulation, to caudal fin control.



Fig. 6. ?*Callopterus*; CM 5013; Kimmeridgian, Solenhofen, Bavaria.

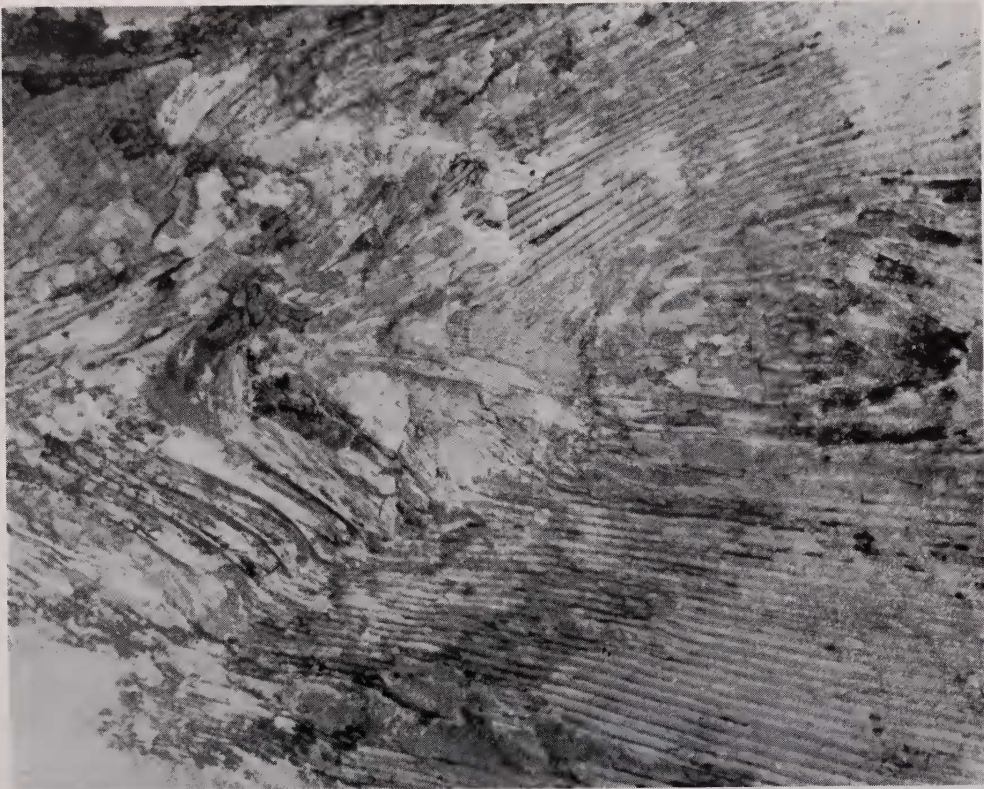


Fig. 7. *Sauropsis curtus*, Type; CM 4772; Kimmeridgian, Solenhofen, Bavaria.



Fig. 8. *Pachycormus esocinus*, CM 5243; Liassic, Holzmaden, Germany.

By contrast, we have seen that in the caturoid amioids, where vertebral centra are either totally lacking, as in *Caturus*, or lacking in the upturned caudal axis, as in ?*Callopterus* (fig.6), varied specializations of the caudal skeleton toward a more powerful propulsive system are evident. Although in these fish it is not possible to find centra, and thus evidence of doubled hypurals, one hypural is always expanded to a greater degree than the others in the series. The expanded hypural will always be the first hypural dorsal to those supporting the ventral lobe of the caudal fin. Correlated with this structural modification is the presence of a deeply forked caudal fin, a member that will not be affected by the turbulence set up by swimming motions of the body.

The caudal fin of the caturoids, then, is divided into discrete dorsal and ventral lobes, separated by a series of short, highly branched and articulated fin-rays composing the central region. Musculature originating on the broadest hypural will be anchored more strongly than the equivalent musculature in the eugnathoid amioids. The presence of this musculature, coupled with the arrangement of the fin-rays of the dorsal lobe, would produce unified action of the dorsal lobe of the caudal fin in power swimming. The various means of stiffening the caudal peduncle in turn would provide a rigid lever with the principal fulcrum forward of the peduncle. The extra rigidity of the caudal peduncle seems to be the key factor in power swimming. The specializations within the caudal skeleton themselves divide the caudal fin into discrete dorsal and ventral lobes. Undulatory motion of the caudal fin in the caturoids is effectively eliminated as a significant propulsive device.

A similar series of adaptations has evolved independently in the teleosts. It is necessary, however, in discussing teleost caudal skeletons to discuss some of the intricacies of caudal-skeletal terminology that have found their way into the recent literature. The terminology in use here will follow that of Whitehouse (1910), for reasons discussed below.

Two principal terminologies for elements of the teleostean caudal skeleton have been introduced in recent years, that of Gosline (1960, 1961), and that of Nybelin (1963). The greater clarity of Nybelin's terminology seems to have won for it the most widespread acceptance. Neither terminology however, takes into account functional aspects of the fish tail as does the terminology of Whitehouse. As a result, inconsistencies of usage of modern terminologies are becoming increasingly frequent (Cavender, 1966).

The function of the caudal-fin skeleton is to support the caudal fin.



Fig. 9. *Leptolepis dubia*. CM 4845; Kimmeridgian, Solenhofen, Bavaria.

It would therefore be most logical to identify all elements concerned with this function.

Nybelin (1963, fig. 1) bases his terminology upon aspects of the anatomy of the tail that are modified by function, such as the site of emergence of the caudal artery from the haemal canal. Whereas hypurals have been logically defined as those haemal elements that support caudal fin-rays (Whitehouse, 1910: 592), Nybelin defines hypurals as those haemal elements located to the rear of the emergence of the caudal artery from the haemal canal. This point varies greatly in the teleosts, but in all the lower teleosts occurs rearward of those elements supporting the lower lobe of the caudal fin, i.e. at the level of occurrence of the double hypural on a single centrum (fig. 9). The terminology of Nybelin thus excludes between three and five specialized haemal elements from consideration as part of the caudal skeleton.

All but a very few of the ventral fringing rays of the caudal fin are supported upon more or less specialized haemal spines. Or conversely, haemal spines that support fin-rays are *ipso facto* specialized, as this phenomenon occurs only in the caudal fin. To discuss intelligently the structure, function, and evolution of the caudal fin it is necessary to give these specialized haemal spines a collective name. It is unnecessary to define hypurals differently from Whitehouse (1910). A hypural is thus a haemal spine at the caudal end of the fish, the function of which is to support a caudal fin-ray or rays. The first hypural would be, in this manner, the first haemal spine in rearward progression to support a caudal fin-ray. The first ural centrum, then, is the centrum supporting the first hypural element.

As the epurals of Nybelin and previous authors are incontrovertibly interdorsals (Whitehouse, 1910), a definition of epurals as those interdorsal elements that support a caudal fin ray or rays would be the only one consistent with the remainder of caudal-fin terminology.

There remains the problem of the uroneurals, or urodermals, or orordermals (Whitehouse, 1910; Nybelin, 1963; Cavender, 1966). These bones are lateral, long, straplike ossifications in the caudal region of the teleosts. They are located within or mesial to the deep musculature of the tail. They may attach at their front ends to either epural bases, hypural bases, or ural centra, varying with the systematic position of the particular group of fish. The primitive arrangement seems to be one uroneural per ural vertebra. Also termed uroneurals by Nybelin (1963), but more correctly termed orordermals (Patterson, 1967), or urodermals (Gosline 1961) are a series of superficially situated ossified tendons.

These structures found in caturoid fish (Nybelin, 1963, figs. 13, 15) and questionably in some lower teleosts, are neither homologous nor analogous to the structures known as uroneurals in the teleosts.

The origin of the teleostean uroneurals will not be known with certainty until careful embryologic work has been done. Observation of the caudal skeletons of many Jurassic teleosts, however, gives enough information for an educated guess.

The uroneurals are not dermal structures derived from scales. They are located deep within the caudal musculature, and are covered by an intact squamation in all known cases. They are not neural arches, specialized or unspecialized, as, primitively, each vertebral segment with a uroneural also bears a neural arch. It is possible that in the salmonoid fish, fusion of a neural arch element with a uroneural may take place in the embryo. Several Jurassic teleosts however, show intermediate stages in the development of a salmonoid type of uroneural from a primitive strap-shaped uroneural.

The uroneurals of the teleosts arise *de novo*, and are exclusively a teleostean innovation. They occur in the same relationship to caudal vertebral centra as do intermuscular bones with respect to centra of the trunk, namely in epineural, epicentral, or epipleural position. In some groups of teleosts, such as the Cretaceous Pachyrhizodidae, Y-shaped uroneurals are found, quite similar to the Y-shaped intermuscular bones known in some recent teleosts. With the exception of the Liassic Pholidophoridae, which have intermuscular bones (Lund, 1966) but no uroneurals, all lower teleosts with uroneurals also have intermuscular bones, and uroneurals cease to be present in the teleosts at the same evolutionary level as do intermuscular bones. This level occurs where vertebral specializations in trunk and tail are advanced enough to take over the function of these bones.

Only one known fossil fish not commonly considered as teleostean in relationship possesses uroneurals. This fish is *Eurycormus speciosus* Wagner. Neither the original description of the species (Wagner, 1863: 97) nor the author's illustration serves to distinguish this fish from a member of the Leptolepids. And Nybelin's (1963, p.502) illustrations of the caudal skeleton of specimens supposedly pertaining to this species tends to confirm, rather than deny, the possibility that this fish has been incorrectly designated as an amioid.

There is sufficient correspondence in characters between uroneurals and intermuscular bones to warrant the hypothesis that uroneurals are intermuscular bones of the caudal region, modified in connection with



Fig. 10. *Leptolepis dubia*. CM 4714; Kimmeridgian, Solenhofen, Bavaria.

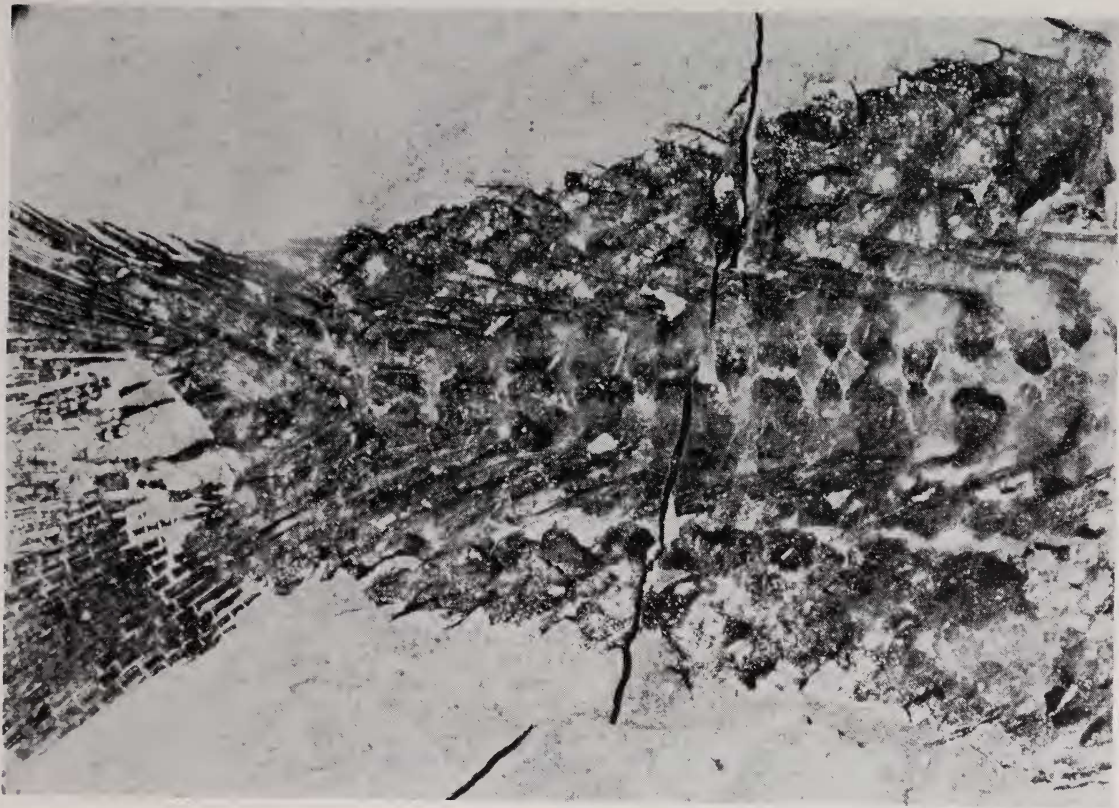


Fig. 11. *Pholidophorus bechei*. AMNH 6300; Lower Lias, Dorsetshire.

the functioning of the teleost tail. They may be defined as lateral bones of segmental arrangement associated with the caudal skeletons of primitive teleosts.

The caudal skeletons of the earliest teleosts show many adaptations from a basic structural plan. The basic arrangement is most evident among the Liassic Pholidophoridae. Thin ring-centra, diplospondylous in the anterior caudal series, are holospondylous in the ural series and do not continue into the upturned body axis (fig. 12). All hypural elements supporting the ventral lobe of the caudal fin are expanded relative to the haemals more toward the front of the series. These hypurals are appressed and joined at their bases by peg-and-socket articulations. The most broadly expanded hypural lies just rear of the last ural centrum although it may have been associated with a spur-shaped centrum (fig. 12). Beyond this point, a series of eight or more small hypurals, of decreasing length, lie encased by fin-rays of the dorsal lobe of the caudal fin. Dorsally, the neural arches of four to six segments to the rear of the last ural centrum are greatly thickened and expanded and overlap each other (figs. 11, 12). All but the most rearward of the neural arches bear a thin neural spine.

The pholidophorid axial skeleton is a loosely associated series of dorsal and ventral hemicentra, with complete freedom of lateral motion as far back as the first ural centrum. This loose association of vertebral elements anterior to the tail indicates that lateral undulation was capable of playing a significant part in normal propulsion. The caudal skeleton, on the other hand, is clearly divided into functional dorsal and ventral lobes, and undulatory motion of the ural centra is restricted further by peg-and-socket haemal processes. This adaptation of the tail for unified, as opposed to undulatory action, permits short bursts of speed to be delivered from motion of the caudal fin, in excess of speeds possible from a simple caudal fin such as is present in *Amia*.

The caudal skeletons of the closely related leptolepoid lineages differ in three particulars from those of the pholidophorids: ossified vertebral centra in the upturned body axis, one ural centrum which supports two hypurals, and uroneurals present lateral to the ural vertebrae.

Leptolepis dubia from the Kimmeridgian of Solenhofen, Bavaria, illustrates the basic type of leptolepoid tail well. In this fish, five ural centra are present, including the last, conical centrum. Thirteen hypurals are present, seven of which are dorsal to the ultimate centrum and are totally encased in fin rays in the undisturbed tail (fig. 10). The penultimate centrum supports two hypurals, which in members of the



Fig. 12. *Pholidolepis dorsetensis*. MCZ 3209; Lower Lias, Dorsetshire.

family Leptolepidae are fused at their bases. Three epurals are present, supported upon greatly reduced neural arches and in turn supporting fringing rays (fulcra) of the caudal fin. Six straplike uroneurals are present, the first short, the second through fourth long and uniformly narrow, the fifth broad at the rear, and the sixth quite thin. All but the sixth originate high on their respective ural centra, at the bases of the neural arches, in an epineural position (fig. 9).

The caudal skeleton of the Leptolepidae differs very little from that of the Liassic Pholidophoridae. Variations within the leptolepoid-thrissopid-elopid group of Jurassic fishes show patterns that can easily be derived from a caudal skeleton close to that of *L. dubia*. Although detailed analysis of the variations among the Jurassic teleosts is beyond the scope of this paper, for present purposes it can be said that the basic pattern of the teleost caudal skeleton is one very similar, morphologically and functionally, to that of the *Leptolepis-Pholidophorus* tail.

Sustained swimming speed or extreme power in swimming is not necessarily advantageous to a fish. Long ranging, open-sea fish of predacious habit, such as the modern Tuna and Swordfish, require maximum speed and power. For the vast majority of fish habitats, such extremes of speed or power are necessary only to escape from predators, and the adaptations required for sustained high-level function would actually be a hindrance during normal life activities. The development of a functionally homocercal tail in the earliest teleosts provided them with a propulsive system able to meet greater demands upon it than any other propulsive system at the time. The versatility of the teleostean caudal skeleton was a very important factor in the rapid radiation of the teleosts during the Mesozoic.

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